

Does the microarchitecture of Mexican dry forest foliage influence spider distribution?

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Abstract. Spider species diversity has been associated with vegetation structure and stratification but there are few studies comparing the spider distribution in different shrubs and trees. In this study we analyzed the species distribution of the spider community of 11 shrub and tree species in two different study sites in a Mexican tropical dry forest. We present results from multivariate analyses that explain their distribution. A classification analysis based on spider abundances separated one shrub, *Croton ciliatoglanduliferus*, from the rest of the plant species. This was explained by the presence of large numbers of the oxyopid *Peucetia viridans* (Hentz 1832) on this plant. A second cluster segregated broad-leaved from small-leaved, bipinnate species. This was mainly due to higher spider abundances in the latter type of plants. Four vegetation variables were estimated and their influence on the species distribution was assessed by means of a principal components and regression analysis. With the exception of *P. viridans*, all spiders were positively associated with number of leaves and number of branchlets per 50 cm branch and negatively with foliage area.

Keywords: Community ecology, species abundances, plant structure

Habitat structure is an important factor that influences diversity, abundance, and distribution of spider species (Lubin 1978; Hatley & MacMahon 1980; Evans 1997; Whitmore et al. 2002). The available evidence has been gathered from both natural communities (e.g., Lubin 1978; Robinson 1981; Raizer & Amaral 2001) and agricultural systems (Rypstra et al. 1999; Samu et al. 1999). Habitat structure and complexity are related to factors such as prey abundance, shelter against enemies and suitable microclimatic conditions (Riechert & Tracy 1975; Gunnarsson 1996; Halaj et al. 1998; Raizer & Amaral 2001). Habitat preferences, however, can be highly specific and species belonging to different guilds have particular requirements according to their morphological, physiological, and behavioral features (Turnbull 1973; Wise 1993).

Variation in plant height, foliage density, leaf surface area, number of leaves and branchlets, and number and type of inflorescences, can affect the abundance and distribution of foliage-dwelling spiders (Hatley & MacMahon 1980; Evans 1997; Halaj et al. 1998; Uetz et al. 1999; Raizer & Amaral 2001; Corcuera et al. 2004; Heikkinen & MacMahon 2004; Souza & Martins 2004, 2005). In this study, we evaluated the influence of plant architecture on the spider community by means of multivariate and regression analyses. We analyzed the abundance of foliage spiders and four plant attributes of 11 of the most abundant trees and shrubs found in a tropical dry forest in western Mexico.

Information on Mexican spiders is widely dispersed. After extensive bibliographical research, Jiménez (1996) found 7,916 species. It is not known how many specimens were collected from foliage since most studies were concerned with taxonomy (Jiménez 1996). There have been a few reports on foliage spiders on cacao and coffee plantations (Ibarra Núñez et al. 1995, 1997; Moreno-Molina et al. 2001; Pinkus-Rendón et al. 2006), but these studies concentrate on species richness and diversity. Besides a diversity analysis (Corcuera et al. 2004), to our knowledge nothing has been written on the distribution of foliage spider communities in dry forests.

METHODS

Study sites.—Tropical dry forests cover 42% of the tropical and subtropical land area on the planet (Murphy & Lugo 1986). The dominant plant species are strongly drought deciduous (Mooney et al. 1989). In Mexico, they are the prevailing vegetation type along the west coast and cover ca. 12.4% of the country's area (Arizmendi et al. 1990). Mexican tropical dry forests are found between 0 and 1990 m elevation (Rzedowski 1978). Mean annual temperature ranges from 20 to 29°C, and mean annual precipitation from 300 to 1800 mm (Rzedowski 1978). Dry forests are strongly seasonal, with a long dry season and intense rainy season (Rzedowski 1978; Murphy & Lugo 1986).

The study sites are located in the Municipality of Villa Corona in the state of Jalisco (20°20'N, 103°35'W). Altitude above sea level is 1640 m. Mean annual temperature was 20.3°C and mean annual precipitation from the last 15 years was 826 mm. Most of the rain falls between mid-June to mid-September and there are between 6 and 8 dry months each year.

Plant variables.—Eleven trees and shrubs were sampled in two sites (El Caracol and Charco Verde) to test the effect of plant architecture on the distribution of foliage spiders: *Bursera schlechtendalii*, *B. bipinnata*, *Guazuma ulmifolia*, *Heliocarpus appendiculatus*, *Ipomoea wolcottiana*, *Prosopis juliflora*, *Mimosa galeotti*, *Lysiloma acapulcense*, *Croton ciliatoglanduliferus*, *Acacia cymbispina*, and *Byrsonima* sp. (Table 1). These plant species are typical of Mexican dry and thorn forests and were the most common shrubs and trees in the study sites (Table 2). Details about plant cover estimation are given elsewhere (Corcuera & Butterfield 1999; Corcuera & Zavala-Hurtado 2006).

Foliage area, number of leaves and number of branchlets (i.e., small branches) were determined for each plant species. The sample unit was a 50 cm terminal branch from a limb rising horizontally from the center of the plant (McCaffrey et al. 1984). Foliage area was measured by drawing the contour

Table 1.—Mean (\pm SD, $n = 10$ per species) of plant height, foliage area, number of leaves and branchlets on a 50 cm terminal branch ($n = 3$ per species) for 11 species in two dry forest sites, El Caracol and Charco Verde, in the Municipality of Villa Corona, Jalisco, Mexico. * = small-leaved species.

Plant species	Code	Plant height (m)	Foliage area (cm ²)	Number of leaves	Number of branchlets
<i>Bursera schlechtendalii</i>	Busc	3.4 (0.32)	850 (386.1)	70.0 (28.28)	22.5 (6.4)
<i>Bursera bipinnata</i> *	Bubi	3.4 (0.71)	541 (140.3)	2473.2 (2692.16)	22.0 (9.9)
<i>Croton ciliatoglanduliferus</i>	Crci	1.1 (0.32)	1026 (631.8)	28.0 (16.17)	9.0 (4.2)
<i>Guazuma ulmifolia</i>	Guul	4.8 (0.98)	3349 (989.7)	45.8 (19.30)	21.5 (0.7)
<i>Acacia cymbispina</i> *	Accy	3.3 (0.71)	120 (27.6)	10670.4 (2313.43)	10.5 (4.9)
<i>Prosopis juliflora</i> *	Prju	3.9 (1.25)	242 (105.1)	6696.0 (2136.01)	11.0 (0.7)
<i>Byrsonima</i> sp.	Bysp	2.7 (0.70)	1712 (1065.1)	64.5 (21.71)	15.0 (4.2)
<i>Ipomoea wolcottiana</i>	Ipwo	5.0 (0.72)	2556 (960.2)	12.2 (7.79)	11.0 (2.1)
<i>Heliocarpus appendiculatus</i>	Heap	5.3 (0.67)	2050 (975.0)	15.0 (7.53)	8.0 (1.4)
<i>Lysiloma acapulcense</i> *	Lysp	4.4 (0.47)	340 (105.9)	30240.0 (11671.35)	11.5 (3.5)
<i>Mimosa galeotti</i> *	Miga	2.7 (0.48)	320 (209.6)	16301.0 (5250.44)	11.5 (7.8)

of all leaves present on the branch on millimetric paper with 1 mm divisions. The procedure was repeated on three branches for each species and the mean area (cm²) per branch was calculated. Mean number of leaves, or leaflets for bipinnate species, and branchlets per branch was obtained from the three samples of each species. Plant height was recorded in a sample of 10 individuals for each species. All plant variables were averaged from measures from both sites.

Spiders.—Spiders were collected by branch beating (Southwood 1978) in June, July, September, October, and November 1999, and January and April 2000. For each plant species, a terminal branch was chosen and beaten 10 times with a cane (trial samplings showed that more strokes did not dislodge more specimens) (Southwood 1978; McCaffrey et al. 1984). This procedure was repeated on 10 individuals of each plant species in each of the seven visits to each site. The specimens were collected in 60 cm diameter muslin covered trays. Two persons collected the spiders from the canvas using tweezers and manual aspirators. McCaffrey et al. (1984) found that this technique efficiently sampled the arachnofauna of foliage dwelling spiders. The number of individuals for each spider species (11 plants \times 7 dates) was added in order to execute the analyses, and the results were log transformed to obtain a normal distribution. The specimens were preserved in 70% alcohol and identified later at the Centro de Investigaciones

Biológicas (CIBNOR) in La Paz, Baja California. Voucher specimens have been deposited in the collection at the Laboratorio de Ecología Animal, UAM-Iztapalapa, México City.

Multivariate analyses.—We analyzed the spider community similarities with a classification using an unweighted pair group average method with percent similarity. A Principal Components Analysis (PCA) was used to analyze the distribution of spider species in relation to the plant species. Regressions were used to assess the relationship between the main PCA axes and the plant variables. The classification and ordination analyses were carried out using the statistical software MVSP 3.2 (Multivariate Statistical Package; Kovach 1999).

RESULTS

Plant variables.—Foliage area was greater for broad-leaved trees. *G. ulmifolia* had the largest area (3349 cm²), followed by *I. wolcottiana* (2556 cm²), and *H. appendiculatus* (2050 cm²). *Croton ciliatoglanduliferus* and *Byrsonima* sp. had intermediate foliage areas (1026 cm² and 1712 cm², respectively); both are broad-leaved shrubs. All small-leaved species had much lower foliage areas (Table 1).

Lysiloma acapulcense and *M. galleotti*, small-leaved species, had the highest mean number of leaves per terminal branch

Table 2.—Plant cover percentage and spider abundance and richness of 11 trees and shrub species in two dry forest sites, El Caracol (C) and Charco Verde (V), in the Municipality of Villa Corona, Jalisco, Mexico. * = small-leaved species.

Species	Plant cover (%)		Spider abundance		Spider richness	
	C	V	C	V	C	V
<i>Bursera schlechtendalii</i>	0.6	2.7	49	31	9	9
<i>Bursera bipinnata</i> *	2.9	3.3	68	84	11	11
<i>Croton ciliatoglanduliferus</i>	9.9	0.8	87	83	11	6
<i>Guazuma ulmifolia</i>	2.3	5.4	28	29	7	11
<i>Acacia cymbispina</i> *	31.1	23.2	128	108	12	9
<i>Prosopis juliflora</i> *	4.8	0.5	70	119	10	11
<i>Byrsonima</i> sp.	4.8	1.6	43	27	12	7
<i>Ipomoea wolcottiana</i>	16.0	6.0	35	35	8	8
<i>Heliocarpus appendiculatus</i>	1.9	7.9	32	45	10	6
<i>Lysiloma acapulcense</i> *	2.9	18.8	53	65	10	11
<i>Mimosa galeotti</i> *	11.6	4.9	74	47	11	10
Other plant species	11.1	24.8	—	—	—	—
Total	100	100	667	673	—	—

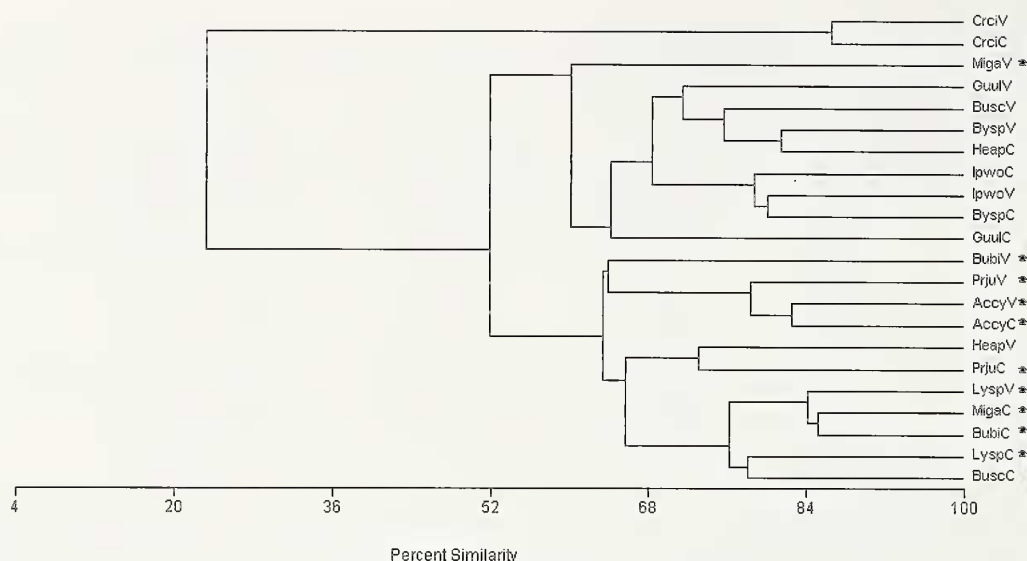


Figure 1.—Classification of 11 plant species in two sites according to spider species abundance. Plant codes are the same as in Table 1. The additional last capital letter represents the sample site (C = Caracol, V = Charco Verde). * = small-leaved species.

(30,240 and 16,301, respectively), while the broad leaved trees, *H. appendiculatus* and *I. wolcottiana*, had the lowest number of leaves (15 and 12.2, respectively) (Table 1). Mean number of branchlets per terminal branch was higher for *B. schlehtendalii* (22.5), *Bursera bipinnata* (22), and *G. ulmifolia* (21.5), while *C. ciliatoglanduliferus* (9) and *H. appendiculatus* (8) had the lowest values (Table 1). Mean plant height among species varied from 1.1 m (*C. ciliatoglanduliferus*) to 5.3 m (*H. appendiculatus*) (Table 1).

The dominant species in both sites was *A. cymbispina*, a shrub that grows in areas that have been altered by cattle and goat grazing. In both sites, *P. juliflora* was the second most abundant species. *C. ciliatoglanduliferus* is an invasive shrub particularly common in one site (El Caracol). In this site *M. galeottii* was also dominant, while *L. acapulcense* was common in Charco Verde (Table 2).

Spider abundance and composition.—A total of 1340 adult spiders belonging to 21 species were caught in the two sampled sites (667 in El Caracol, and 673 in Charco Verde) (Table 2). Species composition was similar in both sites. *Isaloides cf. yolotli* (Jiménez, 1992), *Hamataliwa puta* (O. Pickard-Cambridge 1894) and *Peucetia viridans* (Hentz 1832) represented 73% of the total numbers caught in El Caracol and 69% in Charco Verde. Four species were represented by only one individual: *Micrathena gracilis* (Walckenaer 1805) and *Mallos* sp. in El Caracol, and *Euryopsis californica* Banks 1904 and *Ocrepeira* sp. in Charco Verde. The other species found were *Neoscona oaxacensis* (Keyserling 1864), *Euriophora edax* (Blackwall 1863), *Wamba crispulum* (Simon 1895), *Theridion* sp., *Mimetes puritans* Chamberlin 1923, *Tmarus ehecaltoatl* Jimenez 1992, *Misumenoides* sp., *Modysticus cf. floridana* (Banks 1895), *Apollophanes punctipes* (O.P.-Cambridge 1891), *Philodromus albicans* O. Pickard-Cambridge 1897, *Oxyopes bifidus* F.O. Pickard-Cambridge 1902, *Phidippus* sp., *Paramarpissa piratica* (Peckham & Pekham 1888) and *Metaphidippus cf. apicalis* F.O. Pickard-Cambridge 1901.

In both study sites, the dominant families were hunters, in particular Oxyopidae with 49% and 43% (El Caracol and

Charco Verde, respectively), followed by Thomisidae (36% and 38%). The family Salticidae was represented by 10% and 11% of the total catch. In spite of spiders being sampled from the foliage, web weavers were only represented by 1.5% of the total catch in El Caracol, and 5.1% in Charco Verde.

Spider species distribution.—A classification of the plants based on the spider abundances resulted in three main clusters at the 50% similarity level (Fig. 1). The first cluster separated *C. ciliatoglanduliferus* (Crci) from all other plant species. The second cluster included all the broad-leaved species with the exception of *M. galeottii* (MigaV) from Charco Verde, while the third cluster included all the small-leaved plants and two broad-leaved trees, *H. appendiculatus* (HeapV) from Charco Verde and *Bursera schlehtendalii* (BuscC) from El Caracol. The first division was explained by the presence of *P. viridans*, one of the most abundant species, which was found almost exclusively on *C. ciliatoglanduliferus*. Most spiders had higher abundances in small-leaved plants (Table 2), which explains the separation between the second and third clusters (Fig. 1).

The first two PCA axes based on spider abundances accounted for 88% of the variance (58% and 30%, respectively). Since some spider species had less than 5 individuals, only 15 out of 21 species were included in the analysis. Nine of these species were common to both sites. The first axis of the ordination (eigenvalue = 0.58) was negatively correlated with plant height ($r = -0.87$, $P < 0.001$). The ordination along this axis was determined by the large numbers of *P. viridans* on *C. ciliatoglanduliferus* (both had the highest scores on the positive side (Fig. 2). The second axis (eigenvalue = 0.55) was negatively correlated with foliage area ($r = -0.91$, $P < 0.001$) and positively with number of leaves ($r = 0.86$, $P < 0.001$) and branchlets ($r = 0.61$, $P < 0.05$). The ordination pattern along this axis clearly segregated all spider species and small-leaved bipinnate plants from broad-leaved plant species (Fig. 2). Spider species, as well as all small-leaved bipinnate species had positive scores. These plants had a high numbers of leaves and branchlets, and low foliage area (Table 1,

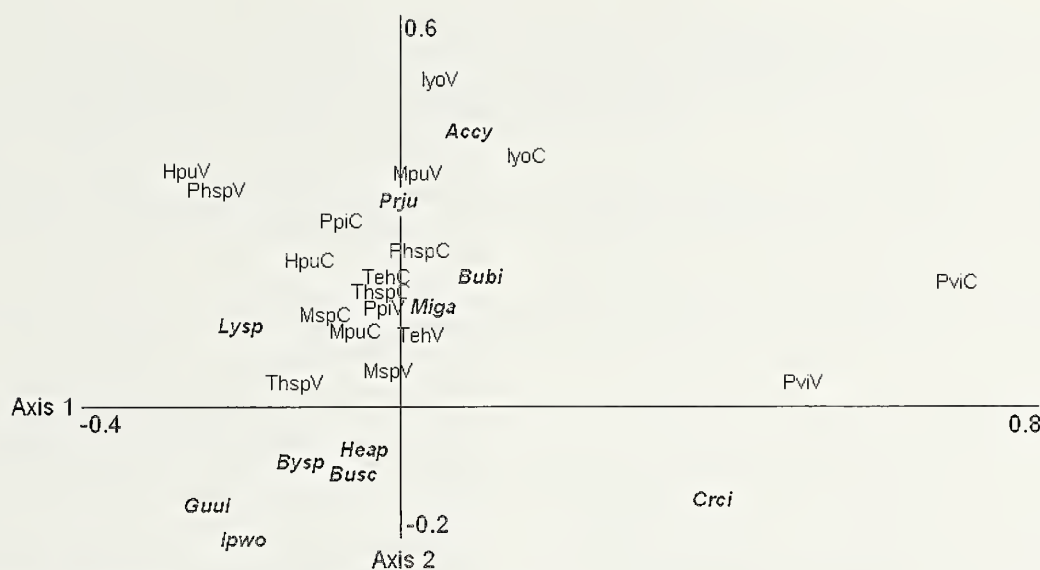


Figure 2.—Principal Components Analysis of the spider species present in 11 dry forest plant species. Spiders are: Pvi = *Peucetia viridans*, Iyo = *Isaloides cf. yollotl*, Hpu = *Hamataliwa puta*, Mpu = *Mimetes puritans*, Phsp = *Phidippus* sp., Ppi = *Paramarpissa piratica*, The = *Tmarus checatlocatl*, Thsp = *Theridon* sp., Misp = *Misumenoides* sp. In the codes for spider species names, the additional last capital letter represents the sample site (C = Caracol, V = Charco Verde). Codes for plant names are in bold and are the same as in Table 1.

Fig. 2). Conversely, the plant species on the negative side included those with high foliage area but low number of leaves and branchlets (Table 1, Fig. 2). The ordination shows the relationship of each spider species with the plants. For instance, *I. cf. yollotl*, a common spider species was particularly abundant on *A. cymbispina* and that is why these species appear together in Fig. 2.

DISCUSSION

In spite of intensive sampling (a total of 1540 branches during a seven month period), only 21 species were found among 1340 individuals collected in the two sampled sites (677 in El Caracol, and 673 in Charco Verde). Rarefaction analyses (P. Corcuera, unpublished results) showed that only two or three additional foliage species are likely to be found in the study area.

Small-leaved plants appear to be suitable sites for foliage spiders. Evans (1997) found that social crab spiders preferred *Eucalyptus* species with smaller leaves. Perhaps more importantly, and regardless of plant taxon, density of leaves per branch (e.g., Gunnarsson 1990; Souza & Martins 2005) as well as structural complexity are better predictors of spider diversity. Branching or twig density, as well as leaf density have been found to be strongly related with number of spiders, diversity, and abundance of various functional groups (Hatley & MacMahon 1980; Halaj et al. 1998; Corcuera et al. 2004). These variables also explained the spider distribution in this study.

A classification of the plant species (Fig. 1) separated most small-leaved bipinnate trees and shrubs from most broad-leaved species. The second axis of an ordination also segregated the plants and gave high positive scores to all spiders and small-leaved plants and negative to all broad-leaved (Fig. 2). This axis was positively correlated with number of leaves and branchlets and negatively with foliage area. The first axis was correlated with plant height and was explained by high numbers of *Peucetia viridans*, a very

common spider in the study sites and the only one that was associated with the small shrub *Croton ciliatoglanduliferus*.

Causal explanations for habitat preferences of foliage spiders have not been explored in depth but some hypothesis have been suggested. For example, *Peucetia* species are known to favor plants with glandular trichomes, presumably because arthropods are trapped by these hairs and represent available prey for the spider (Vasconcelos-Neto et al. 2006). Halaj et al. (1998) suggested that plants with higher cover are easier to locate and might provide more resources. This might explain higher diversities of most spiders on the most common trees and shrubs. Total number of individuals was significantly correlated with plant cover in the two sites ($r = 0.83$, $P < 0.005$ for El Caracol and $r = 0.67$, $P < 0.05$ for Charco Verde). This may explain why *A. cymbispina*, which had the highest plant species cover in both sites, supported high densities of most spiders (Table 2). In the same way, *M. galeotti*, a small-leaved tree from Chaco Verde, was included in the broad-leaved cluster in the classification (Fig. 1, Table 2). This species had low densities of spiders probably because of its low cover in this site. However, *P. juliflora* and *B. bipinnata*, with high richness and species abundances, had very small cover in one or both sites (Table 2). Plants with higher cover might be easier to locate, but they do not necessarily provide more resources. Other factors (i.e., branch and leaf density) appear to be more important to understand the distribution of foliage spiders.

Some plant attributes might provide suitable microclimatic conditions. Riechert & Tracy (1975) suggested that certain plants might be favored because of their ability to modify the thermal environment. In hot climates with long drought periods, preserving body temperature would be a most important factor. Small-leaved plants, especially *C. cymbispina* and *P. juliflora* could provide a cooler environment because they either do not shed their leaves (as does *P. juliflora*) or remain green during the early draught, which is when

spiderlings start to disperse. This species also starts producing leaves early, before the rains, when broad-leaved trees and shrubs are still deciduous. Once settled on these plants, there would be no reason to move to shrubs or trees where conditions would be less favorable.

Besides resource availability and favorable physical conditions, accessibility of refuges against predators plays an important role in determining spider distribution. Gunnarsson (1996) suggested that high leaf densities could provide shelter from bird predation. This would not seem the case in our study sites, since bird attacks tended to be more frequent in small-leaved trees and shrubs (Corcuera 2001), where spiders are more abundant.

Few studies have compared differences in the abundance of spiders on foliage of different shrub and tree species (e.g., Halaj et al. 1998; Raizer & Amaral 2001; Souza & Martins 2004). Although some spider species were found in small numbers (< 5 individuals), and it is not possible to reach any conclusions about their distribution, our results reveal that foliage spider species were positively influenced by small-leaved trees and shrubs with a high number of leaves and branches, and negatively by broad-leaved plants with a high foliage area among 11 plant species of the Mexican tropical dry forest.

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